

- LINHART, S. B. (1973): Age determination and occurrence of incremental growth lines in the dental cementum of the common vampire bat (*Desmodus rotundus*). *J. Mammalogy* **54**, 493–496.
- PARK, H.; HALL, E. R. (1951): The Gross Anatomy of the Tongues and Stomachs of Eight New World Bats. *Trans. Kansas Acad. Sci.* **54**, 64–72.
- PHILLIPS, C. J.; STEINBERG, B. (1976): Histological and scanning electron microscopic studies of tooth structure and thegosis in the common vampire bat, *Desmodus rotundus*. *Occas. Papers Mus. Texas Tech. Univ.* **42**, 1–12.
- PHILLIPS, C. J.; STEINBERG, B.; KUNZ, T. H. (1982): Dentin, cementum, and age determination in bats: a critical evaluation. *J. Mammology* **63**, 197–207.
- NEUWEILER, G.; DALTON, S. (1981): Die Ultraschalljäger. *GEO*, Hamburg, H. 1 (1981), 98–113.
- SCHMIDT, U. (1978): Vampirfledermäuse, Familie Desmodontidae (Chiroptera). *Die Neue Brehm-Bücherei* 515. Wittenberg-Lutherstadt: A. Ziemsen Verlag.
- STORCH, G. (1968): Funktionsmorphologische Untersuchungen an der Kaumuskulatur und an korrelierten Schädelstrukturen der Chiropteren. *Abh. Senckenberg. naturforsch. Ges.* **517**, 1–92.
- VILLA, R. B. (1966): Los murcielagos de Mexico. Mexico: Univ. Nacional Autonoma de Mexico.

Anschrift des Verfassers: Dr. HENNING VIERHAUS, Teichstr. 13, D-4772 Bad Sassendorf-Lohne

Communication in the southern Bat-eared fox *Otocyon m. megalotis* (Desmarest, 1822)

By J. A. J. NEL and M. H. BESTER

Mammal Research Institute, University of Pretoria, Pretoria

Recept of Ms. 25. 10. 1982

Abstract

Use of visual, vocal, olfactory and tactile communication of bat-eared foxes in the Kalahari desert were related to their social organization and environmental features. Family groups forage close together and visual signalling predominates; vocalizations are few and soft, while urine marking increases in frequency in winter during pair-formation or reinforcement of existing pair bonds.

Introduction

The bat-eared fox is a small social canid, widespread in especially the drier areas of southern and eastern Africa. It favours short grass habitat and feeds primarily on insects, preferentially on termites *Hodotermes mossambicus* (NEL 1978; LAMPRECHT 1979). Subspecies occur in southern and eastern Africa, and in both areas a wide range of documented and potential predators and competitors exist.

Communication in bat-eared foxes has probably evolved in conjunction with their lifestyle and is adapted to enhance individual fitness in a particular habitat. Environmental differences would therefore, as in other aspects of their ecology and behaviour, be reflected in the method and frequency of use of a particular method or channel, of communication. Differences in the behavioural ecology of bat-eared foxes in eastern and southern Africa have been documented (NEL 1978; LAMPRECHT 1979) and differences in communication patterns can be expected. This paper gives an inventory of the ways in which the southern subspecies communicate, the context in which these occur and the constraints that operate, and briefly compares it to described communication in the East African form.

To understand the context of the communication methods of the foxes we studied, we

give a short summary of their lifestyle and annual cycle. Bat-eared foxes form monogamous pairs which persist for at least a year, possibly longer. Pair-formation occurs in winter (June–July), young are born from October–December in our study area, and nuclear family groups stay together for up to 7 months, till break up occurs in June–July. Sibling groups can possibly stay together for longer, and breeding starts at an age of ca 18 months. In our main study area (the southwestern Kalahari) territoriality is absent and groups intermingle freely while foraging, which obviously reduces the need for ways of advertising territories. In addition, in an environment with very high diurnal summer temperatures, and where bat-eared foxes are normally diurnally active except in mid-summer, normal physiological constraints place a limit on the use of e.g. urine in olfactory communication. Other moulding factors in the communicatory pattern of the bat-eared foxes we studied are their habit of group foraging, with members rarely > 200 m and usually < 30 m apart in open terrain, resting together and frequent allogrooming.

Only the communicatory patterns perceivable by us are given below and those listed must be regarded as being a minimum count, while some nuances in graded signals probably also escaped our notice.

Study area and methods

Data reported were mostly obtained in the Kalahari Gemsbok National Park, a 9454 km² area in the southwestern Kalahari with a rainfall of 200–250 mm per year. Topographically it consists of duneveld, with long usually parallel dunes up to 15 m high covered with grass, shrubs (e.g. *Rhigozum trichotomum*) and scattered trees; and the bare beds of two normally dry rivers. Merging into the riverbeds are low-lying flats, often with a good grass cover of low-growing *Stipagrostis obtusa* and small *R. trichotomum*. For a detailed description of the vegetation see LEISTNER (1967). Data accrued in the course of an ongoing study on foraging behaviour and communicatory behaviour was only occasionally specifically studied, resulting in small sample sizes for some actions. The number of animals studied, duration and distance followed reflect this. Most data are from free-ranging foxes (ca 48) observed for 87 h 53 min in the bed of the Nossob River, with supplementary information from a captive group (1♂, 2♀) in the National Zoological Gardens, Pretoria. Groups or individuals were followed by vehicle, during summer at night when moonlight or foglamps provided illumination, or by day in winter. Observations were recorded on tape and later transcribed. For logistic reasons data were only obtained in midsummer (December–January) when pairs had cubs at the den or with them foraging, or else winter (July) at or immediately after the time that family groups break up and pairs are formed.

Results

Visual displays

The muzzle, eye region and especially the ears (large, and top borders fringed with black contrasting hair to the lighter insides) as well as the black-tipped tail with its dorsal longitudinal black stripe are conspicuously marked and provide important sources of visual signals.

The behavioural context, and the different parts of the body involved during displays are (see also Table 1):

Agonistic

1. Facial displays (Figs. 1 and 2)

a. Head up (Fig. 1a and b). Head held high, eyes open, ears erect and directed forwards, mouth closed. Used when looking intently at object (another fox or jackal some distance away). With increasing alertness (e.g. close proximity of conspecific) the base of the ears are closer together. In threat situations accompanied by arched neck, back and tail.

b. Head forward (Fig. 2a and b). Head held slightly lower, with ears turned sideways and pulled slightly sideways or back. Mouth closed. Body often in a crouched position. Used, for example, on approach by a conspecific.

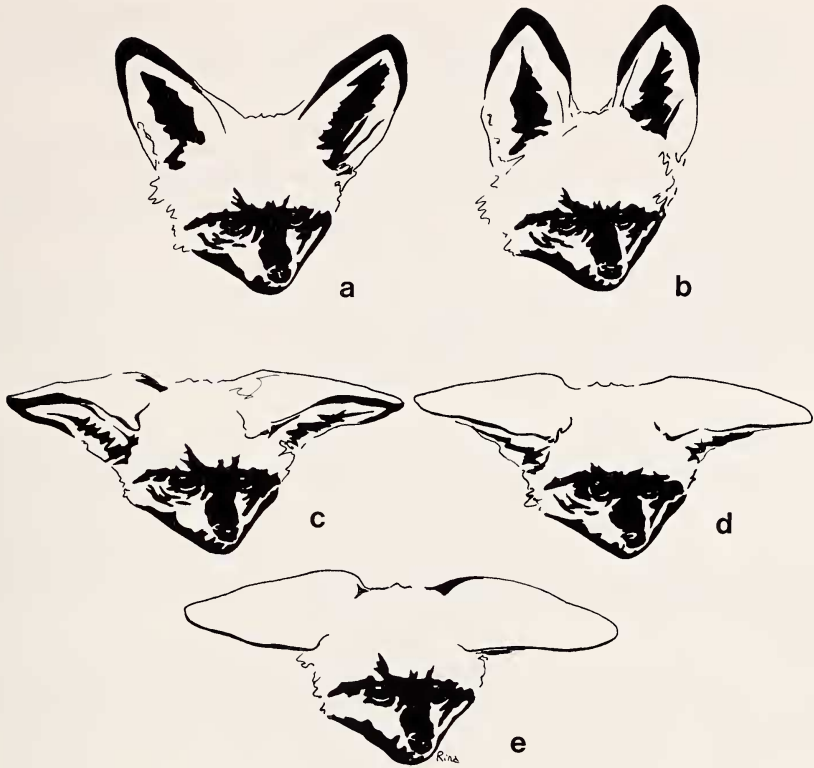


Fig. 1. Facial displays of the bat-eared fox: a = head up; b = head up, at increased alertness; c-e = gape; note change in ear position as intensity increases from c-e

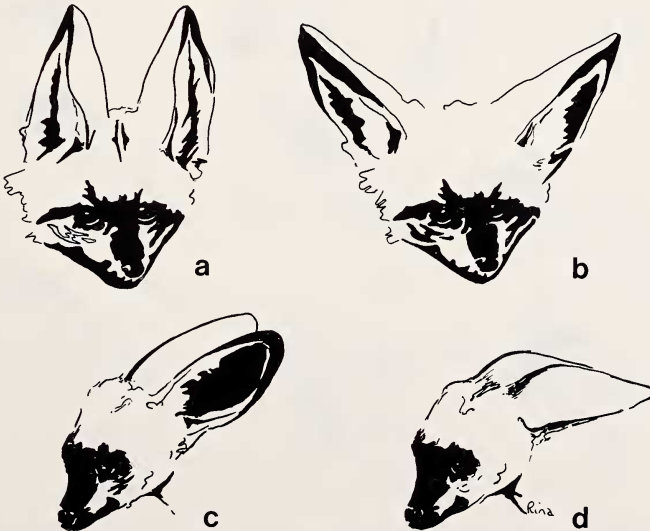


Fig. 2. Facial displays of the bat-eared fox: a = head forward; b = head forward, but change in ear position probably correlates with change in motivation state; c and d = ears back

c. Gape (Fig. 1 c-e). Head held low, ears pulled sideways and down, mouth slightly open ("defensive gape threat"). Animal still crouching and may growl softly. Before the mouth opens the upper lips are slightly puckered. Given, for example, on very close approach of a conspecific.

d. Ears back (Fig. 2c and d). Head held low (when individual is lying down, can be close to or on ground) with ears pulled right back against head. Given when showing fear or submission, e.g. on approach of predator (brown hyaena *Hyaena brunnea*) or another fox. This display can grade into a grin, with the head still low, or turned sideways (see inguinal presentation below), mouth slightly open, lips pulled back, and teeth showing: the latter in cases of extreme submission.

These displays are graded, with various combinations of ear and lip positions probably relating to motivational thresholds; the above descriptions are thus somewhat arbitrary points in an aggressive-defensive continuum (Figs. 1 and 2). An individual when approached by man usually gives a short bark and takes flight following position c above.

2. Tail Position

The black tip and dorsal stripe of the tail stands out clearly and increases the effectiveness of signalling through different positions, owing to the heightened contrast.

Position of the tail varies from hanging down to erect and arched in an inverted U shape. These positions correlate with increased aggression, dominance or type of activity (Fig. 3). The arched, inverted tail position (Fig. 3h) is especially evident in dominance, threat or aggressive encounters, or sexual arousal (see also KLEIMAN 1967). It also occurs, however, during play and defaecation.

An erect tail, with tip at an angle of 45°, (Fig. 3j) is very occasionally seen and seems to function as a "rallying" signal, when a group is foraging and especially playing, in long grass or shrubs. Straight horizontal tail positions are found only in contexts such as running, chasing other species (e.g. black-backed jackals *Canis mesomelas*), flight or in

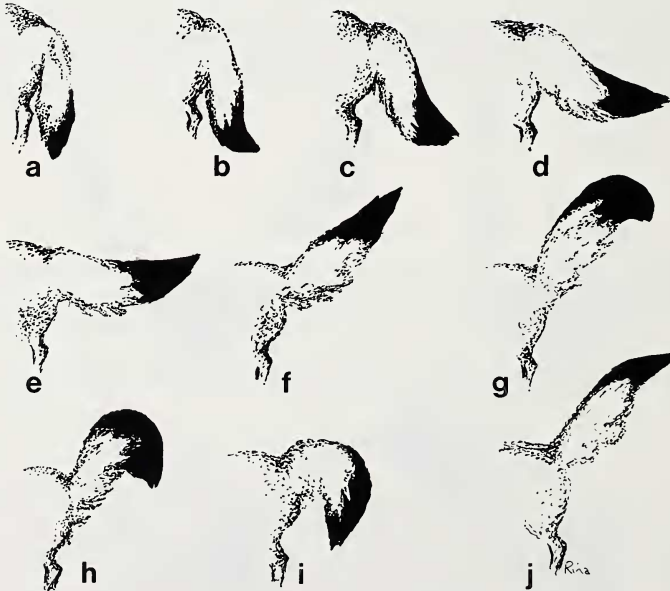


Fig. 3. Tail positions of the bat-eared fox: a-h = change in position related to increase in aggression or dominance; e = horizontal tail; h = inverted U tail; i = inverted tail during defaecation; j = pointed tail

Table 1

Number and context of different visual displays by bat-eared foxes during summer and winter in the southern Kalahari

See text for description of displays

Displays	No. observed		Situation eliciting display	Result
	Summer	Winter		
Head forward ¹	11	2	Approach of possible predators; vehicle	Signaller usually moves off; other group members become attentive
Gape face ^{1,2}	11	7	Meeting other foxes; approach of predators; when approaching other fox with food; close approach of vehicle	Lessens aggression of receiver; can be followed by signaller adopting arched tail, grin
Grin	1	2	When threatened; during inguinal presentation	Signaller can run away
Arched neck and back ¹ (in conjunction with arched tail)	4	–	Approach of jackal, strange fox	Jackal retreats
Arched tail (Agonistic context)	13	3	Approach of jackal, brown hyaena; meeting other foxes; smelling paste marks of brown hyaena; smelling inguinal region of ♀	Jackal run off; other foxes move away; ♀ urine-marks
(Play context) ³	8	–	Group-mates playing; to solicit play	Play ensues
(Elimination)	17	9	Physiological need to defaecate	? Stimulation of others to defaecate
Pointed tail	3	3	Invitation to play; to rally group members on sudden appearance of possible predator	Other rush to join signaller; join group
Tail flick (modified wag)	7	–	Cubs to ♂ when greeting, during play, when being chased; when surprised by jackal	Play continues
Pilo-erection ¹	1	–	Threatening possible predator (jackal)	Jackal moves off
Crouch/crawl	6	–	♀ approach ♂/♂ threatened by other ♂ with cubs	♂ allogroom ♀; ♂ sniffs inguinal region of ♀ and sits down next to ♀; greeting; receiver sniffs signaller, bites him, signaller runs off
Play bow	2	–	To elicit play	Play ensues
Inguinal presentation	3	–	♀ when threatened by strange ♂/♂ towards other ♂	♂ sniffs region, then moves on, ♂ sniffs region, then neck; two ♂♂ then forage together
Total	87	26		
No/h	1,26	1,20		

¹ Also interspecifically. – ² Could also function to make fox less visible, when combined with lying down curled up. – ³ In group context – single score or whole or part of group playing.

submission (when it is held flat to the ground). The tail is never tucked between the hindlegs, even in cases of extreme submission. Tail wagging is absent, except in cubs (see also BERRY 1978), although a modified form of wagging occurs when the tail is erect (KLEIMAN 1967). However, as this occurs in play, it can also function to assist rapid turning of a running individual; when being chased (by conspecifics or predators) the tail can be rapidly flicked to one side, especially when making sharp and abrupt turns in an emergency.

3. Body Postures

a. Arching of the neck and back, in conjunction with an erect head, can occur when threatening conspecifics or individuals of other species. In a defensive threat context the back can remain arched but the head is then lowered, neck extended, and ears pulled back. A variation of this posture, with ears cocked forward, mouth opened, occurs when cubs attempt to follow an adult from the den. This seems to coerce the cubs to return to the den, but whether only a purely visual signal is involved, or a very soft vocalization as well, is unknown.

b. Crouch: forepart of the body is lowered, forelegs stretched out, and back part of body raised, head low and ears pulled sideways or back. This posture, which is common to most canids as a submissive display, also occurs when eliciting play, ("bow" of LEHNER 1978) and here could function as metacommunication; often play-fighting follows. This posture is occasionally used in greeting (contact behaviour), sometimes in exaggerated form with the body supine and tail stretched out straight behind – a typical belly-crawl.

c. Inguinal presentation, by a submissive individual. The animal rolls over onto its side and then back, with uppermost back leg pulled back to expose the inguinal region, and head turned sideways. More commonly performed by females towards strange males, than between males. This display also occurs during play (see also LAMPRECHT 1979).

4. Piloerection

In extreme cases of threat piloerection of hair on the neck, shoulder, rump and tail can occur, thereby increasing the visual size of the individual. Piloerection invariably occurs only in conjunction with an arched neck, back and tail, and is directed commonly towards possible predators, e.g. black-backed jackals.

Play

Both adults and young play, after a rest or in the course of foraging. Play can be in brief bouts, or up to a few minutes in duration. Many of the signals described above in agonistic situations also occur in the context of play: the erect or pulled-back ears; arched tail; crouch; etc. In play, however, a body posture absent in the previous context occurs: the head is held high, but the ears are pulled back somewhat or sideways; back and tail arched, and gait a stiff-legged walk.

Greeting

Greeting involves visual, tactile and probably also olfactory signals. Bat-eared foxes seem able to recognize individuals up to 30 m away, and either ignore them, stare intently (and sometimes approach closely) or attack without any preliminary displays.

The approach display functions as a symbolic token of submission (LE CLUS 1971) in greeting between pair mates or group members and during courtship. It is a low intensity submissive display by the approaching individual which keeps its head slightly lowered, neck extended, ears pulled back and muzzle orientated towards the mouth corner of the other individual. This display is received by a head high, tail down posture. During courtship this display is accompanied by a raised tail. "Greeting" by nuzzling the tip of the mouth is common.

The supine body position or belly-crawl (see above) is also used in the context of greeting; although submissive in nature, it was used by the ♀ of a mated pair when approaching the male guarding the young.

Vocalizations

Bat-eared foxes in the Kalahari seem to use few loud vocalizations, and these somewhat sparingly as in East Africa (LAMPRECHT 1979). Vocalizations are either approach-eliciting or contact calls, or else warning (agonistic) calls. Those in the first category are all soft, and do not function over any distance (cf. howls of black-backed jackals) so cannot be used as a spacing mechanism. The high-pitched and penetrating warning and mobbing calls on the other hand occur very infrequently.

Nine vocalizations are recognised and described in Table 2. It is probable that this Table is an over-simplification and more intensive study should further refine the categories given (see e.g. LAMPRECHT 1979). As many vocalizations are soft and unobtrusive they are easily missed; also no communal vocalizations occur.

The approach-eliciting whine (contact whine of LAMPRECHT 1979) is used to call cubs from the den to the adult lying outside, or when moving off from the den, or to call the

Table 2

Bat-eared fox vocalizations and their behavioural context¹

Vocalization	Context	Distance	Volume
A. Contact			
soft whine/mew	calling cubs or mate to follow/contact/during grooming	short-medium	low
woof/growl/hiss	warning cubs/warning grooming	short	low
short whistle	grooming	short	low
chirping call	deserted cubs/cubs separated from each other	short-medium	low
B. Agonistic:			
growl/snarl/hiss	defence/agonistic/when threatened or chased	short	medium
snarl/yap	agonistic	medium	medium-high
scream/distress cry	when wounded	long	high
short bark	warning/when surprised/when threatened	long	high
high-pitched bark	mobbing call	long	high

¹ Pers. obs. and data from LAMPRECHT (1979) and BERRY (1978).

cubs to follow an adult into the den. It is used as well between adults foraging some distance apart, especially to "call" one to a productive food patch.

The bark is usually directed at conspecifics or competitors, but so far we have not heard it being given towards possible predators. It is uncommon, and usually uttered when conspecifics from other groups approach a den with cubs too closely. The high-pitched mobbing bark is used when black-backed jackals approach a den with young cubs, (when this bark causes nearby pairs of foxes to start running towards the pair defending their den) and when mobbing brown hyaenas (MILLS 1978). In captivity, when competing for favoured food items in short supply, members of a group softly snarl, growl or hiss at each other; when actually fighting the growling is louder and they also yap and hiss.

Scent-marking

Urine, faeces and glandular secretions are commonly used by mammals for scent-marking specific objects or areas, but for canids data are mostly on urine-marking and to a lesser extent faecal-marking (e.g. KLEIMAN 1966; HENRY 1977; MACDONALD 1979 a and b, 1980; ROTHMAN and MECH 1979; BOWEN and COWAN 1980; WELLS and BEKOFF 1981).

Urine-marking

Postures adopted by bat-eared foxes when urinating are the FLU (forward lean urination), RLU (raised leg urination), and SQU (squat urination). During urination for presumably physiological reasons (urine not directed to a particular object, or previous urination – KLEIMAN 1966) the FLU is commonly used by males, and the SQU by females (see also LAMPRECHT 1979). When marking (directing urine onto a particular object, previous urination or faeces) males assume the RLU, and females the SQU. No vertical objects were ever seen to be marked. Scratching never occurred before or after urine-marking, in contrast to coyotes (WELLS and BEKOFF 1981), nor did rolling in or next to the urination ensue.

In the field marking was observed rarely in summer (4,8 % of urinations, $n = 21$), and more often in winter (56,5 % of urinations seen, $n = 23$). Marking sometimes comprised double marking (38,5 % of markings seen, $n = 13$), with the female marking first, followed by the male (i.e. a SQU followed by a RLU). Only once was defaecation (DEF) of a female followed by a male RLU over it. Single animals were only very infrequently observed and no cases of marking seen; marking thus only was found in pairs or larger groups. Double marking ensued both between presumably incipient pair members, and in groups of up to four subadults (see also LAMPRECHT 1979). Urine-marking also occurred on its own, never (as far as we could determine) in conjunction with glandular marking, or scratching, and very seldom with defaecation, in contrast to the situation in coyotes (BOWEN and COWAN 1980). The stimuli eliciting marking by females were presumably the close attention of the male, and for double marking by the male the urination of the female.

Even though urination (and defaecation) took place sometimes immediately, sometimes 5 min and > 100 m away following encounters with strange (non-group member) foxes, interactions were normally minimal and it is doubtful if these encounters served to elicit marking – the frequency did not increase after such encounters. Another stimulus, only seen once, was a fresh paste-mark of a brown hyaena which elicited jumping, snapping at it, and finally RLU marking by a male.

Only once was a male seen to sniff the dark spot, mid-dorsally, on the female's tail, before double-marking. Whether this dark spot contains a supra-caudal gland is unknown. Whether some marking was elicited by previous urination before our observations is doubtful, as in an arid environment evaporation of these would be rapid.

As found by LAMPRECHT in East Africa urination, whether incidental or for marking, occurred anywhere in the home range.

Frequency of urination differed markedly between summer (0,4 urinations km^{-1} , or 0,16 fox- km^{-1} and $0,39 \text{ h}^{-1}$) and winter (1,7 urinations km^{-1} , or 0,6 per fox- km^{-1} with 1 urine-mark km^{-1} or 1,13 urinations including 0,7 urine-markings h^{-1}). During July 1980 in two groups of respectively five and six foxes frequent double-marking between a male and female occurred – once, over 0,6 km moved in 1 h marking took place five times; on another occasion over 2 km moved in 3 h 15 min the pair marked nine times. This no doubt can be related to the role played by urine-marking in pair formation (cf. ROTHMAN and MECH 1980 for wolves) and secondly the lower ambient temperature. On the other hand during summer foxes were followed mostly at night, which could have led to some urinations passing unnoticed.

In the captive group only urine-marking was observed. The ♂ marked throughout the year, in the following situations:

1. Smelling (and then marking) a marking spot
2. after smelling a female's vulva
3. after self- or allogrooming
4. after smelling a conspecific urinating, and then smelling the urine
5. after eating
6. after having a fright
7. after an aggressive interaction
8. after walking around for a while

Marking took place at three localities in the enclosure but were most frequent at one. Again no vertical objects were marked (see also KLEIMAN 1966), and a SQU was always assumed. The females only started marking when coming into oestrus, but this did not raise the frequency of male marking. Females marked far less (1,2 and 0,4 day⁻¹ vs. 8 day⁻¹) than the male. No rolling occurred after defaecating but one female did roll in the other's urine.

Defaecation

Defaecations were more common than urinations both in summer and winter (Table 3) and could therefore better serve a communicating function. Defaecation took place anywhere on the home range, resulting in single scats, or near the burrow (see also BERRY 1978) or resting spot, resulting in "extended" middens with numerous scats (> 30) in an area of ca 20–30 m². Whether this can be construed as a "latrine" is doubtful. From a den containing 10 foxes (2 adult, 8 young) in February 1976, individuals would move 20 m away upwind and defaecate in quick succession following emergence in the afternoon and before leaving to forage. On other occasions this same group (and others, on other occasions) only defaecated some 10–15 min and > 200 m away from the den. While defaecating, both sexes assume the squat position, with the tail either horizontally behind the animal, or slightly lifted at the base but dropping to the ground, or more usually raised in the inverted U position, in which case it could serve as a visual display for social stimulation since a chain reaction (defaecation by other members) then usually ensued. Single scats ensuing from group defaecations therefore were deposited throughout the home range, but in different parts on different days.

Table 3

Comparison of the use of different types of communication by bat-eared foxes in the Kalahari

Communicating channel	No. and frequency/h			
	No.	Summer Frequency	No.	Winter Frequency
Olfactory				
Urinations	20	0.29	9	0.40
Urine-marking	1	0.02	14	0.20
Defaecation	49	0.71	25	1.11
Visual	87	1.26	27	1.20
Vocal	7	0.1	8	0.36
Tactile	48	0.70	18	0.80
Total	212	3.08	101	4.49

Multiple defaecating bouts by an individual are common, especially after leaving a den containing cubs when 2–3 defaecations, usually 3 bouts/5 min, close to (< 50 m) of the den would result. Defaecations followed by urinations were only observed when adults left a den or resting spot.

Glandular secretions

The use of glandular secretions in communication by *Otocyon* is unknown. Scratching apart from digging for food is absent; thus whether interdigital glands play a role (if at all present) is obscure. It is also doubtful if the hair split on the back contains a gland, used when rolling – LAMPRECHT (1979) found no signs of a gland in this region, and areas rolled on are very seldom sniffed at afterwards.

In bodily contact, however, smells could be important. Physical contact occurs primarily in approach situations, or when resting together. Inguinal presentation during submission, followed by a sniff of this region by the dominant fox, occurs very infrequently.

Tactile communication

Huddling by cubs and adults are common, as are allogrooming, both between young and adults, and adults throughout the year (see also KLEIMAN 1967; LAMPRECHT 1979). During huddling the chin of one fox often rests on rump of another, and in allogrooming more attention (64.9 % of noted allogrooming, $n = 57$) is given to the face, with its contrasting marking (found also by KLEIMAN 1967 but not by LAMPRECHT 1979). Nuzzling of the mouth (licking and nibbling nuzzle) of parents by cubs, especially when the adults return to the den occurs, but as no regurgitation of food to the young has ever been noted (see also LAMPRECHT 1979) this behaviour probably functions as an approach/greeting display, as it is also carried into adulthood. According to LEHNER (1978) this behaviour (face-licking) in the coyote is a submissive display that has evolved from food-begging in the neonate.

Nuzzling of the inguinal region of the female by the male was only noted in the context of pair formation (no matings were seen).

Contactual-circling and standing-over, as found in e.g. coyotes (LEHNER 1978) was never observed.

Table 4

Tactile communication in bat-eared foxes in the Kalahari

Behaviour	No. observations		Context	Result
	Summer	Winter		
Muzzle licking (nuzzling)	7	–	Cub greeting parents	Sometimes play ensues; allogrooming of cubs by parents; suckling
Allogrooming	23	8	When joining up with pair members of group, during huddling and in pair-bonding	Reciprocal allogrooming, probably reassurance
Huddling ¹	1	14	Possible thermoregulatory role	? Lessen heat loss of individuals
Biting	4	–	Chasing jackals off den with cubs	Jackals flee
Snapping	13	2	Disputes over ownership of food items, ♀ to discourage suckling attempts by cubs	Gape, crouch by receiver; cub moves to ♂
Jumping/pawing ¹	2	–	During play	Play continues
Total	50	24		
No/h	0.73	1.07		

¹ In group context – single score for whole of part of group participating.

The body or hip-slam only occurred when bickering over food, especially in captivity and very occasionally in the field (only noted on two separate occasions) and during play. In the latter instance the motivation eliciting the slam is probably different, as before play metacommunication occurs. During aggression one fox will grab the other by the scruff of the neck or shoulder, may snap at it and bite; this can also occur interspecifically. During play foxes can rear on the hindlegs and paw at each other (see also LAMPRECHT 1979).

Discussion

The bat-eared fox is a canid with a large repertoire of often graded signals. Among the foxes it is the most gregarious (KLEIMAN 1967). The differences in social groupings in summer (parents with small cubs, often at a den) and winter (break up of nuclear family group into a pair and probably sibling group) is to some extent reflected in the differences in frequency of communication types – olfactory communication, especially marking, is virtually absent in summer and much more prevalent in winter. Similarly the frequency of vocalizations is much higher in winter (Table 3). It is possible that these two means of communication are more valuable in pair-bonding than the others, which show nearly equal frequencies in the two broad seasonal categories.

Some years ago KLEIMAN (1967) suggested that the more social canids can be expected to have a wide range of visual signals (the prediction that less social canids should have a reduced range has not been substantiated) and this is certainly the case in the bat-eared fox, where especially ear and tail positions are flexible along a continuum, in all probability affording a finely graded series of messages as in other social canids e.g. the coyote *Canis latrans* (LEHNER 1978) and wolves *C. lupus* (SCHENKEL 1947). Contrasting colouration (black fringed ears, facial markings and black-tipped and dorsally-striped tail) and both head and tail displays would enhance the visual impact and thus effectiveness of signal transfer. Of all visual signs changes in tail position is most obvious and common, followed by varying the position of the ears. The raised position of the tail, in conjunction with the contrasting markings, constitute an obvious and effective visual signal; however, if a dorsal tail gland is present this position could enhance odour-dispersal (KRUK in litt). As in other canids, e.g. the coyote (LEHNER 1978), erect ears signify heightened interest, and aggression, while pulled back ears denote submission. In conjunction with the head elevation and extension, tail position and general body posture finely graded variations in agonistic content can thus be expressed. Eyes and mouth seem to play a subservient role in this species.

Some signals could also have evolved through ritualization into displays e.g. the arched, inverted U shape of the tail, raised to avoid soiling when defaecating, but used now in other contexts as well. Similarly some signals or displays may have different meanings according to the context in which they occur as, for example, the crouch which can occur in agonistic encounters, contact/greeting between pair members, and play solicitation, in which case it can also function in a metacommunicative way.

Although the bat-eared fox uses a number of vocalizations these are for the most part soft contact or approach-eliciting sounds which do not carry far (see also LAMPRECHT 1979). In the first instance vocalizations would evolve in adaptation to the group-living social system, where group members usually den or rest together, and forage in company although spread out. In the southwestern Kalahari territoriality is absent and therefore vocal spacing mechanisms do not operate – there are no communal vocalizations, and the only loud barks are in response to predators; fighting is rare in nature. The higher incidence of calling in winter (Table 3) probably also, as e.g. in the black-backed jackal (SKEAD 1973) coincides with a peak in sexual activity (pair-formation), but not in territory establishment, as this is absent in Kalahari *Otocyon*.

As in previous studies (KLEIMAN 1966; LAMPRECHT 1979) urine-marking was found to occur nearly exclusively during the pair-bonding period, with double markings occurring, usually with the male overmarking the urination of the female on elevated objects such as a grass tuft or low shrub. Double markings were far less frequent (38,5 %) than in other canids, e.g. the coyote (ROTHMAN and MECH 1979) although also in the context of pair-formation, and also less than found by LAMPRECHT (1979) for bat-eared foxes in the Serengeti. No "handstands" as in red foxes *Vulpes vulpes* (MACDONALD 1980) or golden jackals (GOLANI and MENDELSSOHN 1971) were ever seen. However, both urine-marking and "non-marking" urinations are infrequent, but more common in winter. We suggest that in our study area normal physiological constraints of semi-deserts operate as free water is scarce, and that little liquid waste-products are available. In winter with lower diurnal temperatures (when the foxes are active) this constraint will be somewhat less. This is supported by the findings that defaecations are much more common. Again, the use of urine-marking of territorial boundaries or routes is absent in contrast to golden jackals *Canis aureus* (EISENBERG and KLEIMAN 1972; MACDONALD 1979b), but agreeing with the finding of LAMPRECHT (1979) in Serengeti, and urinations occur throughout the home range. We have never observed foxes to scratch in conjunction with urinations, urine-marking or defaecation thereby visually strengthening an olfactory signal as in dogs or coyotes (BEKOFF 1979; WELLS and BEKOFF 1981). There is also no evidence that bat-eared foxes use urination to mark food-depleted areas, or mark food sources such as the red fox (HENRY 1977).

Total urinations therefore, including urine-marking, is fairly infrequent ($< 1 \text{ h}^{-1}$) compared to wolves which encounter a scent-mark every 2–3 min (PETERS and MECH 1975) or coyotes which encounter a scent-mark every 3–4 min (BOWEN and COWAN 1980). The low frequency of encountering such scentmarks, whether deposited specifically or incidentally, by foxes in the Kalahari would greatly reduce their communicative value.

The habit of a group defaecating near a den or resting spot would olfactorily advertise important areas in the home range. On several occasions cubs were seen to run to a particular area 20 m away from the den to defaecate; even though the inverted U tail could serve as a social stimulation this would not necessarily mean all members would defaecate in the same small area unless the "extended midden" served some purpose. As with urination, single defaecations were not deposited along home range boundaries (and these are very fluid), in contrast to e.g. golden jackals (MACDONALD 1979b) or pathways (KLEIMAN and EISENBERG 1973). Rather defaecations by bat-eared foxes were concentrated near the "core" of the home range and not the periphery. Bat-eared fox defaecations were always on the bare ground and never on elevated structures such as grass tufts, as is common by the sympatric territorial black-backed jackal.

Thus whether defaecation, apart from elimination, had a marking function is not clear. Haphazard deposition apart from near dens or resting spots, and the absence of the need for territorial demarcation (in contrast to the golden jackal – see MACDONALD 1979b) mitigate against such a function. On the other hand anal gland secretions could increase the scent of defaecations, especially when concentrated near dens and resting spots, thus advertising important parts of the home range.

The other two sympatric canids, the black-backed jackal and silver fox *Vulpes chama* are both less gregarious (mated pairs, single individuals respectively) than the bat-eared foxes but both exhibit a range of visual displays (FERGUSON 1978, 1980; BESTER 1982) and both are more vocal. The black-backed jackal is territorial and communal howling in this species probably serves as a spacing mechanism. In the Serengeti, on the other hand where the bat-eared fox and black-backed jackal are also sympatric, the latter never howls; here howling is often performed by the golden jackal which often occurs together with the black-backed jackal (KRUUK in litt.).

It would seem therefore that the use of specific communicatory channels in the bat-

eared fox in the Kalahari can be correlated to its lifestyle – cohesive and persistent groups, non-territoriality with subsequent few agonistic encounters, foraging in open terrain and normally very low levels of humidity, and the preference for a diurnally-active prey, the harvester termite. Thus olfactory communication is somewhat reduced compared to territorial canids in temperate regions, as are loud vocalizations, and emphasis is put on a graded range of visual displays.

Acknowledgements

We thank the National Parks Board and the National Zoological Gardens, Pretoria, for permission to work in areas under their jurisdiction, and Drs. HANS KRUIK, JÜRIG LAMPRECHT and M. G. L. MILLS and Prof. JOHN SKINNER for many useful comments on previous drafts of this manuscript. During this study BESTER was in receipt of a Council for Scientific and Industrial Research bursary.

Zusammenfassung

Kommunikation beim südlichen Löffelhund, Otocyon m. megalotis (Desmarest, 1822)

Optische, akustische, chemische und taktile Kommunikation freilebender Löffelhunde der südwestlichen Kalahariwüste und von einer kleinen, in Gefangenschaft lebenden Gruppe wird beschrieben.

Es wird ein weites Spektrum visueller Zeichen benutzt; Ohren, Körper und besonders die Schwanzhaltung spielen eine herausragende Rolle. Kontrastierende Haarfärbung der Ohränder und des Schwanzes betonen dieses Organe. Die Haltung des gehobenen Schwanzes in Form eines umgekehrten U ist sehr kennzeichnend für diese Tiere; sie kommt bei agonistischen Zusammentreffen und während des Spiels vor. Schwanzwedeln tritt nur bei Welpen auf.

Vokalisationen sind meistens leise und fungieren in Annährungs- und Begrüßungssituationen. Kommunale Vokalisationen kommen nicht vor, und laute Rufe werden nur beim Vertreiben von Feinden oder Einschüchtern von Artgenossen geäußert.

Olfaktorische Markierung kommt selten vor, und die Frequenz von Urinmarkierung ist im Winter (wenn die Paarbildung stattfindet) viel größer als im Sommer. Es wird angenommen, daß die geringe Frequenz von Urinmarkierung mit dem Fehlen von Territorialität zusammenhängt. Defäkation kommt häufiger vor als Urinieren, und ausgebreitete Kothaufen befinden sich in der Nähe von Lager- und Rastplätzen.

Zwischen Gruppenmitgliedern werden sehr oft Körperpflegehandlungen beobachtet, im Gesicht häufiger als an anderen Körperregionen.

References

- BEKOFF, M. (1979): Ground scratching by male domestic dogs: a composite signal. *J. Mammalogy* **69**, 847–848.
- BERRY, M. P. S. (1978): Aspects of the ecology and behaviour of the bat-eared fox, *Otocyon megalotis* (Desmarest, 1822) in the upper Limpopo River valley. Unpubl. MSc. thesis, Univ. Pretoria.
- BESTER, J. L. (1982): Die gedragsekologie en bestuur van die silwervos *Vulpes chama* (A. Smith) met spesiale verwysing na die Oranje-Vrystaat. Unpubl. MSc. thesis, Univ. Pretoria.
- BOWEN, W. D.; COWAN, I. McT. (1980): Scent marking in coyotes. *Can. J. Zool.* **58**, 473–480.
- EISENBERG, J. F.; KLEIMAN, D. G. (1972): Olfactory communication in mammals. *Ann. Rev. Ecol. Syst.* **3**, 1–32.
- FERGUSON, J. W. H. (1978): Social interaction of black-backed jackals *Canis mesomelas* in the Kalahari Gemsbok National Park. *Koedoe* **21**, 151–162.
- (1980): Die ekologie van die rooijakkals *Canis mesomelas* Schreber, 1773 met spesiale verwysing na bewegings en sosiale organisasie. Unpubl. MSc. thesis, Univ. Pretoria.
- HENRY, J. D. (1977): The use of urine marking in the scavenging behaviour of the red fox (*Vulpes vulpes*). *Behaviour* **61**, 82–106.
- GOLANI, I.; MENDELSSOHN, H. (1971): Sequence of precopulatory behaviour of the jackal (*Canis aureus* L.). *Behaviour* **38**, 169–192.
- KLEIMAN, D. G. (1966): Scent marking in the Canidae. *Symp. zool. Soc. Lond.* **18**, 167–177.
- (1967): Some aspects of Social behaviour in the Canidae. *Amer. Zool.* **7**, 365–372.
- KLEIMAN, D. G.; EISENBERG, J. F. (1973): Comparisons of canid and felid social systems from an evolutionary perspective. *Anim. Behav.* **21**, 637–659.
- LAMPRECHT, J. (1979): Field observations on the behaviour and social system of the bat-eared fox *Otocyon megalotis* Desmarest. *Z. Tierpsychol.* **49**, 260–284.
- LE CLUS, F. (1971): A preliminary, comparative investigation of feeding, communication and reproductive behaviour in *Vulpes chama* (A. Smith) and *Otocyon megalotis* (Desmarest). Unpubl. BSc. Hons. project, Rhodes University.

- LEHNER, P. N. (1978): Coyote communication. In: *Coyotes, Biology, Behaviour and Management*. Ed. by M. BEKOFF. New York: Academic Press. 127–162.
- LEISTNER, O. A. (1967): The plant ecology of the southern Kalahari. *Mem. bot. Surv. S. Afr.* 38, 1–172.
- MACDONALD, D. W. (1979a): Some observations and field experiments on the urine marking behaviour of the red fox, *Vulpes vulpes*. *Z. Tierpsychol.* 51, 1–22.
- (1979b): The flexible social system of the golden jackal, *Canis aureus*. *Behav. Ecol. Sociobiol.* 5, 17–38.
- (1980): Patterns of scent marking with urine and faeces amongst carnivore communities. *Symp. zool. Soc. Lond.* 45, 107–139.
- MILLS, M. G. L. (1978): Foraging behaviour of the brown hyaena (*Hyaena brunnea* Thunberg, 1820) in the southern Kalahari. *Z. Tierpsychol.* 48, 113–141.
- NEL, J. A. J. (1978): Notes on the food and foraging behavior of the bat-eared fox *Otocyon megalotis*. *Bull. Carnegie Mus. Nat. Hist.* 6, 132–137.
- PETERS, R. P.; MECH, L. D. (1975): Scent-marking in Wolves. *Am. Scient.* 63, 628–637.
- ROTHMAN, R. J.; MECH, L. D. (1980): Scent-marking in lone wolves and newly formed pairs. *Anim. Behav.* 27, 750–760.
- SCHENKEL, R. (1947): Ausdrucks-Studien an Wölfen. *Behaviour* 1, 81–129.
- SKEAD, D. M. (1973): Incidence of calling in the black-backed jackal. *J. sth. Afr. Wildl. Mgmt Ass.* 3, 28–29.
- WELLS, M. C.; BEKOFF, M. (1981): An observational study of scent-marking in coyotes, *Canis latrans*. *Anim. Behav.* 29, 322–350.

Authors' address: J. A. J. NEL and M. H. BESTER, Mammal Research Institute, University of Pretoria, 0002 Pretoria, South Africa

Behaviour of an expanding population of the Brown bear (*Ursus arctos*) in northern Europe

By E. PULLIAINEN

Department of Zoology, University of Oulu

Receipt of Ms. 27. 1. 1983

Abstract

The behaviour of a brown bear population (*Ursus arctos*) in N Europe was studied in the years 1968–1982 with the help of the Finnish Border Patrol Establishment and local hunters. Finland received an immigration of bears in the 1970s and the early 1980s from the saturated Soviet Karelian population (approx. 3000 ind. around 1980). Continued immigration from Soviet Karelia into Finnish Northern Karelia, Kainuu and Koillismaa caused the bears to move on into the inland areas of Finland, some crossing the whole country from east to west. Bears also appeared in the southeastern frontier area of Finland, and some slight immigration was recorded from the Kola Peninsula into eastern Finnish Lapland. Finland received 682 bears more from its neighbouring countries (mainly Soviet Karelia) than it lost to these countries in the years 1969–1981, a period during which at least 456 bears were killed in Finland. The number of bears in Finland thus increased by about two hundred (to 300–350) during this period. The bears killed in eastern Finland were predominantly males (64.1 % in 1960–1981), and the proportion of cubs killed was 17.8 %. It is assumed that intraspecific aggressiveness (leading especially to sub-adult dispersal) results in emigration, the males being more mobile than the females.